

Temperature-associated population diversity in salmon confers benefits to mobile consumers

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Abstract. Habitat heterogeneity can generate intraspecific diversity through local adaptation of populations. While it is becoming increasingly clear that population diversity can increase stability in species abundance, less is known about how population diversity can benefit consumers that can integrate across population diversity in their prey. Here we demonstrate cascading effects of thermal heterogeneity on trout–salmon interactions in streams where rainbow trout rely heavily on the seasonal availability of anadromous salmon eggs. Water temperature in an Alaskan stream varied spatially from 5°C to 17.5°C, and spawning sockeye salmon showed population differentiation associated with this thermal heterogeneity. Individuals that spawned early in cool regions of the 5 km long stream were genetically differentiated from those spawning in warmer regions later in the season. Sockeye salmon spawning generates a pulsed resource subsidy that supports the majority of seasonal growth in stream-dwelling rainbow trout. The spatial and temporal structuring of sockeye salmon spawn timing in our focal stream extended the duration of the pulsed subsidy compared to a thermally homogeneous stream with a single population of salmon. Further, rainbow trout adopted movement strategies that exploited the multiple pulses of egg subsidies in the thermally heterogeneous stream. Fish that moved to track the resource pulse grew at rates about 2.5 times higher than those that remained stationary or trout in the reference stream with a single seasonal pulse of eggs. Our results demonstrate that habitat heterogeneity can have important effects on the population diversity of dominant species, and in turn, influence their value to species that prey upon them. Therefore, habitat homogenization may have farther-reaching ecological effects than previously considered.

Key words: *Alaska, USA; behavioral adaptation; biocomplexity; habitat heterogeneity; habitat portfolio; life history variation; Pacific salmon; population diversity; rainbow trout; water temperature.*

INTRODUCTION

Spatial heterogeneity in habitat conditions can generate intraspecific diversity through evolution of local adaptations in populations. This process is increasingly jeopardized as humans dampen the mechanisms that generate habitat heterogeneity and directly homogenize populations through factors such as habitat degradation, suppressing disturbance regimes, overexploitation, and the introduction of nonnative species. Rates of decline in population diversity are much faster than those of species diversity (Hughes et al. 1997), so it is critical to understand how intraspecific diversity mediates ecological processes. Recent research in “eco-evolutionary” dynamics shows that population divergence in one species can

significantly alter its relationship with other species, producing geographic variation in the nature and strength of species interactions such as interspecific competition (Hairston 1980) and predator–prey dynamics (Palkovacs and Post 2009). These changes in ecological interactions can in turn affect evolutionary dynamics, driving eco-evolutionary feedbacks in species and ecosystems (reviewed by Post and Palkovacs 2009, Schoener 2011).

Most work in eco-evolutionary dynamics assumes that single populations of one species interact with single populations of another species. Understanding the ecological implications of intraspecific variation becomes more complex when taking into account the asymmetric spatial and temporal scales over which species often occur and interact with each other. For example, a single population of a mobile consumer may exploit several populations of its prey, thereby integrating over their dynamics. Here, the predator is exploiting a portfolio of prey populations and environmental heterogeneity mediates the composition of the portfolio. In this paper, we addressed three important questions on

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this theme. First, how is habitat heterogeneity associated with population diversity of a prey species? Second, how does the population diversity of this species generate heterogeneity in its interaction with its predator? Third, is the predator able to positively exploit heterogeneity in its prey? We show that spatial heterogeneity in stream water temperature is associated with population diversity in a dominant species, sockeye salmon (*Oncorhynchus nerka*), which increases the potential for rainbow trout (*O. mykiss*) to exploit seasonally pulsed food subsidies of sockeye salmon eggs.

Local adaptation to heterogeneous environments has generated high levels of intraspecific variation in Pacific salmon (Hendry and Sterns 2002). Because salmon home to natal habitat with high precision (Quinn et al. 2006), gene flow is spatially restricted, and populations can differentiate substantially within single watersheds. Several studies have shown spatially proximate populations to differ in life history traits such as spawn timing (Quinn et al. 2000, Schindler et al. 2010). Spawn timing in Pacific salmon is influenced by the ambient thermal regime in spawning habitat due to thermal constraints on embryonic development (Olson 1968). Throughout Bristol Bay, Alaska, USA, for example, sockeye salmon spawn in a variety of aquatic habitats, from cool spring-fed streams to the warm shorelines of lakes (Marriott 1964). Across a landscape, thermal heterogeneity generates a mosaic of salmon populations with diverse life history traits, including substantial variation in their spawn timing (Hilborn et al. 2003).

There has been a growing appreciation for the ecological importance of Pacific salmon as resource subsidies in freshwater and terrestrial ecosystems (Gende et al. 2002, Schindler et al. 2003). Because salmon achieve >95% of their growth in the marine environment (Quinn 2005), their anadromous migrations transport nutrients derived from the marine environment to the freshwater systems where they eventually return to spawn and die. These marine-derived nutrients provide a direct energy subsidy to mobile aquatic predators, such as resident fishes and juvenile anadromous salmon in the form of energy-rich eggs and flesh, which are often critical to annual growth (Scheuerell et al. 2007, Denton et al. 2009, Armstrong et al. 2010).

At the watershed scale, where numerous populations of a single species of Pacific salmon spawn during a confined time period, variation in spawn timing may provide mobile consumers such as rainbow trout with increased temporal availability of egg subsidies from roughly one month on a single spawning stream to 2.5 months throughout an entire watershed, provided the predators are able to make directed movements that effectively track the spatial and temporal availability of salmon eggs (Schindler et al. 2010). In effect, habitat heterogeneity may enhance foraging opportunities to mobile predators by producing fine-scale population diversity that extends temporal access to their key prey

resource. Despite our current understanding of the importance of life history diversity of Pacific salmon in maintaining long-term population resilience (Hilborn et al. 2003), and the importance of salmon as subsidies to consumers (Gende et al. 2002), there have been no studies that document consumers moving adaptively to exploit spatial and temporal patterning of salmon subsidies. Here, we sought to test whether life history diversity, expressed as variation in spawn timing, in Bristol Bay sockeye salmon confers benefits to rainbow trout, which rely heavily on the seasonal pulse of sockeye salmon eggs for their annual growth. Our results demonstrate that by influencing the spatial and temporal dynamics of salmon spawning and, hence, availability of egg resources, spatial thermal heterogeneity in streams indirectly affects the foraging strategies of rainbow trout and provides significant energetic benefits to these predators.

METHODS

We used a combination of empirical field observations of sockeye salmon spawn timing and molecular genetics to provide evidence of an association between fine-scale thermal variation in spawning streams and life history variation in sockeye salmon. Additionally, we conducted a comprehensive movement, diet, and growth study on resident rainbow trout to quantify the indirect effects of this temperature-driven life history variation in sockeye salmon on the foraging ecology of rainbow trout that rely on salmon resources for growth.

Site description

This study was conducted in the Wood River system of Bristol Bay in southwestern Alaska, USA (Fig. 1a). The Wood River watershed has numerous small tributaries that drain into five large lakes, which are connected by short rivers. Over the last 50 years, the watershed has had an average annual spawning migration of 1.1 million sockeye salmon (Baker et al. 2006). The spawn timing of sockeye salmon varies among populations, ranging from mid-July to late-August and typically lasting two to six weeks (Marriott 1964). We conducted our study in two third-order tributaries of Lake Nerka, where resident rainbow trout co-occur with sockeye salmon. Hidden Creek and Lynx Creek support rainbow trout populations that comprise >50% of the resident fish biomass during summer months (June–September). In our focal streams, annual returns of spawning sockeye salmon have averaged 2653 individuals in Hidden Creek and 2852 in Lynx Creek since 1946 (Rogers and Schindler 2008). Each stream is fed by a small lake at the headwaters, and then by a cold-water source below. In Lynx Creek, the cold-water source is a free flowing moderate gradient tributary that drains into the main channel 0.5 km below the lake outlet and is deep enough to provide habitat for stream-dwelling trout. In Hidden Creek, the cold-water source is primarily groundwater, and it offers no habitat to trout.

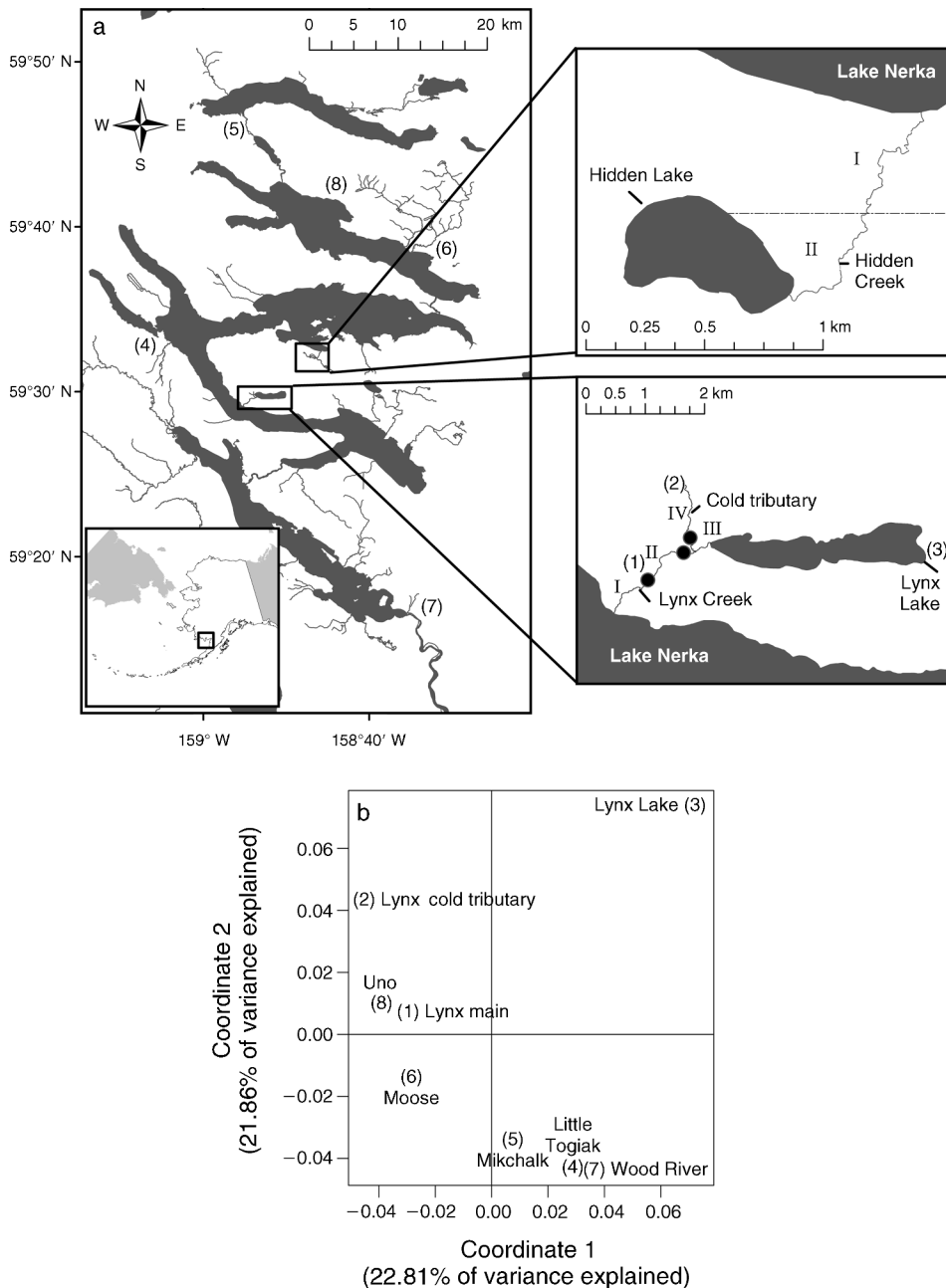


FIG. 1. (a) Map of Bristol Bay, Alaska, USA, at the scale of the Wood River system, showing study streams. Numbers in parentheses indicate individual sockeye salmon populations that were sampled for genetic analyses. The two panels on the right show in finer detail the two study streams where we conducted our rainbow trout movement, diet, and growth studies. In Lynx Creek, the solid circles mark the relative location of each antenna used to quantify rainbow trout movement, which effectively divided the stream into four sections. In Hidden Creek, the horizontal line marks the two equal sections in which we divided the stream for our salmon spawner distribution and rainbow trout diet analyses. (b) Genetic differentiation between three Lynx Creek populations relative to five other populations throughout the Wood River system. Distance between each number represents the results of a principal coordinates analyses of calculated chord distances of the three Lynx Creek sockeye populations and five others throughout the Wood River system. Individual populations are coded by a number in parentheses for geographic reference to the map.

Water temperature

To quantify seasonal summer variation in temperature, we placed iButton temperature loggers ($\pm 1^{\circ}\text{C}$; Dallas Semiconductor, Dallas, Texas, USA) in regions of

each stream that would capture the variation in temperature driven by both cold-water and warm-water sources to each stream. In Lynx Creek, temperature loggers were placed at the lake outlet at the top (section

III), in the cold-water tributary (section IV), and in the lower main channel (section I). In Hidden Creek, temperature loggers were placed at the lake outlet at the top (section II), and below the cold-water spring (section I). Additionally, in late August 2008, we conducted a spatially continuous thermal profile of each stream during midday using a high-resolution thermal sensor data logger (Onset HOB0, Pocasset, Massachusetts, USA) that logged temperature every one second, and linked a time stamp to each data point. A GPS track, set to log every one second, was run simultaneously to synchronize the temperature data to geographic coordinates via associated time stamps.

Life history variation in spawn timing and genetic differentiation between sockeye salmon populations

To quantify the seasonal shift in the spatial distribution of spawning sockeye salmon in Lynx Creek and Hidden Creek, we conducted spatially continuous visual surveys of spawning sockeye salmon in each stream every 10 days in 2008, and every 10 to 20 days in 2009. We surveyed the distribution of adult sockeye salmon with a digital tally counter that recorded the time of each observation. Counts of salmon were synchronized with a GPS track-log and mapped for the spatially continuous temperature data as described in the previous paragraph. We geo-referenced each count to a single reference track of the corresponding stream to compare shifts in the spatial distributions of adult sockeye salmon between different time periods. To quantify variation in the spawn timing between stream sections with different thermal regimes, we divided the streams into two sections. Lynx Creek was divided into two segments, the 3100 m long main channel (sections I through III) and 1700 m long cold tributary (section IV) (Fig. 1a). We divided Hidden Creek into two equal 850-m segments.

We used single nucleotide polymorphisms (SNPs) to determine the degree of genetic differentiation in the early spawning and late spawning populations of sockeye salmon in Lynx Creek (see Appendix C for a detailed description of methodology). Because Hidden Creek fish spawn throughout the stream at a single time, we did not attempt to split them into smaller groups genetically. We obtained fin tissue samples from 95 actively spawning sockeye salmon from eight different stream, river, and beach populations throughout the Wood River system, including the three separate spawning areas of Lynx Creek during summer 2009 (Fig. 1a). Within Lynx Creek, we collected fin tissue samples from salmon spawning in the main channel, the cold tributary, and Lynx Lake beaches.

Field sampling of rainbow trout and analyses of diets

We sampled rainbow trout throughout the two study streams every 7 to 15 days from early June through mid-September to capture seasonal shifts in growth and diet related to each stream region during years 2008 and

2009. Fish were captured using a fine-meshed stick seine and anesthetized using a 50 ppm solution of MS-222 (tricaine methane sulfonate). All individuals were measured to the nearest 1 mm (fork length) and weighed to the nearest 0.1 g. Fish included in the growth and movement study were surgically implanted with coded passive integrated transponder tags (PIT tags; full duplex, 134.2 kHz, 11.5 mm length, 2.1 mm diameter; Allflex-USA, Dallas-Fort Worth Airport, Texas;) into the stomach cavity area (Bond et al. 2007). In Lynx Creek, we tagged 191 rainbow trout in 2008 and 238 in 2009. In Hidden Creek, we tagged 141 rainbow trout in 2008 and 143 in 2009. All captured fish were scanned with a hand-held PIT tag reader for potential recaptures. For each sampling date, we collected diets via gastric lavage from a subset of individuals spanning the observed size range. Diets were enumerated and identified to coarse prey groups in the field. We estimated consumption (milligrams of prey/gram of fish) for all prey items in each diet (see Appendix D for detailed description of methodology). Each batch-processing event was assigned to a stream section to keep track of where individual fish were captured and released.

Rainbow trout movement

We quantified movement patterns of rainbow trout in Lynx Creek in relation to the seasonally variable spatial distribution of adult sockeye salmon using stationary antenna arrays. A PIT tag reader (Allflex-USA, Dallas-Fort Worth Airport, Texas) in each antenna functioned to detect PIT-tagged rainbow trout as they swam by, recording the individual tag ID code, date, and time of detection. Antennas were laid flat along the stream bottom and spanned the entire width of the stream.

We installed single antennas at three locations throughout Lynx Creek that effectively divided the entire stream into four sections based on the location of the cold tributary (section IV) and the distribution of salmon throughout the lower main channel (Sections I and II) (Fig. 1a). Antennas were run continuously from 1 July through 9 September in both years 2008 and 2009. However, due to high stream flows, functionality of the upper antenna site was lost for four days in 2008, and seven days in 2009. Antenna functionality was tested every five to seven days by placing a test PIT tag over an antenna and determining antenna read range. Functionality was determined to be sufficient if read range was at least 30 cm or more above the antenna (stream depth at the antenna sites was nearly always shallower than the read range). Detected movements of individual rainbow trout were assigned upstream or downstream directionality depending on the order in which they were detected swimming across two antennas. We created temporal frequency distributions for both upstream and downstream movements for both 2008 and 2009 by binning fish detections into five-day intervals. Bias for upstream vs. downstream movements by rainbow trout was tested

for by comparing antenna detection efficiencies for confirmed upstream and downstream movements throughout the summer (see Appendix E for a detailed description of methodology).

Rainbow trout growth

We quantified instantaneous growth in mass of recaptured individuals from both Hidden Creek and Lynx Creek if they were recaptured between 15 July and 1 September. During this time period, sockeye salmon were actively spawning in both streams, and sockeye eggs were available for consumption by rainbow trout. Additionally, we only analyzed growth rates of recaptured individuals if the time interval between measurements exceeded 10 days. Instantaneous growth was quantified using the following equation:

$$\text{Growth} = \frac{\ln(\text{mass}_{\text{final}}) - \ln(\text{mass}_{\text{initial}})}{\Delta t}$$

Where $\text{mass}_{\text{final}}$ is the mass at final capture, $\text{mass}_{\text{initial}}$ is the mass at initial capture, and Δt is the duration of time between captures (Ricker 1979).

We stratified our growth analysis to include all recaptures from Hidden Creek, and then divided Lynx Creek fish into two categories, “move” or “stationary,” depending on their observed summer movement trajectory. In Lynx Creek, we assigned movement strategies using two separate but complementary methods. Fish were assigned “move” if they were released initially in sections III or IV after 15 July, and then recaptured in lower sections I or II, or vice versa sometime thereafter between time of initial capture and 1 September. Fish were designated “stationary” if they remained in a single section of stream during the time between recaptures and were not detected moving across an antenna. We confirmed our strategy designations by matching each recaptured individual with its summer movement trajectory provided by the antenna data. We used analysis of covariance (ANCOVA) with $\log_e(\text{initial mass})$ as the covariate to determine the effects of individual movement strategies (Lynx move, Lynx stationary, Hidden) on the relationship between instantaneous growth and $\log_e(\text{initial mass})$. Using the resulting model (ANCOVA, $F_{3,138} = 11.32$, $P < 0.0001$), we simulated instantaneous growth rates for fish ranging between 100 g and 1000 g body mass.

RESULTS

Thermal variation within and between streams

We observed significant differences in the degree of spatial variation in water temperature between Hidden Creek and Lynx Creek during both years of our study such that the additional cold-water tributary in Lynx Creek provided an important layer of habitat complexity compared to Hidden Creek, where there is only a single channel of habitat available to salmon and rainbow trout (Fig. 2a, b; Appendix A: Fig. A1, panels

a–d). While the main channel of both Hidden (sections I and II) and Lynx Creek (Section I through III) exhibited similar seasonal patterns in daily water temperature from late June to early September (average daily stream temperature = 11.2–14.5°C), the cold tributary in Lynx Creek (Section IV) provided consistent cold-water habitat (average daily stream temperature = 5.9°C) that varied little seasonally.

Spatially continuous longitudinal thermal profiles of each stream, collected on a relatively warm and sunny day, revealed similar patterns of cooling from top to bottom such that the main tributary of each stream cooled from 17°C at the top to 14.5°C at the bottom (see Appendix A: Fig. A1, panels e, f). The spatial cooling effect in each stream is consistent with the location of a cold-water input source. However, these profiles revealed that, while the cold-water source in Hidden Creek is due to groundwater seepage into shallow pools ~273 m downstream of the lake (section II), the cold-water source in Lynx Creek is due to the presence of a cold-water tributary 390 m downstream of the lake (Section IV). Indeed, the instantaneous thermal profile of this cold tributary revealed homogeneous stream temperature between 8.3°C to 7.9°C in the afternoon of a sunny day on the date we sampled water temperatures throughout the system. Therefore, in contrast to Hidden Creek, where there is only a single stream channel of habitat, Lynx Creek provides a branched network of stream habitat with seasonally consistent thermal variation that can be used by both salmon and rainbow trout.

Seasonal shifts in the spatial distribution of sockeye salmon

The spatial and temporal patterning of sockeye salmon spawning differed substantially between Hidden and Lynx Creeks, (Fig. 2c; see Appendix B: Fig. B1). In Lynx Creek, we observed seasonal shifts in the spatial distributions of spawning sockeye salmon in both 2008 and 2009, with early-season spawning occurring dominantly in the upper portions of the watershed in the cold tributary and late-season spawning occurring dominantly in the warmer downstream portions. Salmon entered Lynx Creek in mid-July, moved directly through the system, and began spawning in the cold tributary section (section IV). Spawning in the cold tributary lasted for approximately four weeks. Beginning in early August, there was a shift in spawning activity from cold section IV to warmer sections I and II lasting through early September; on 5 September only 2–3% of the total population remained in spawning condition. This spatial and temporal variation in the sockeye distribution corresponded to a temporal separation of ~15 days between peak spawning periods in the cold tributary section (section IV) and the lower main channel of Lynx Creek (sections I and II). Conversely, in Hidden Creek, sockeye entered the stream in late-July and were uniformly distributed throughout the stream from

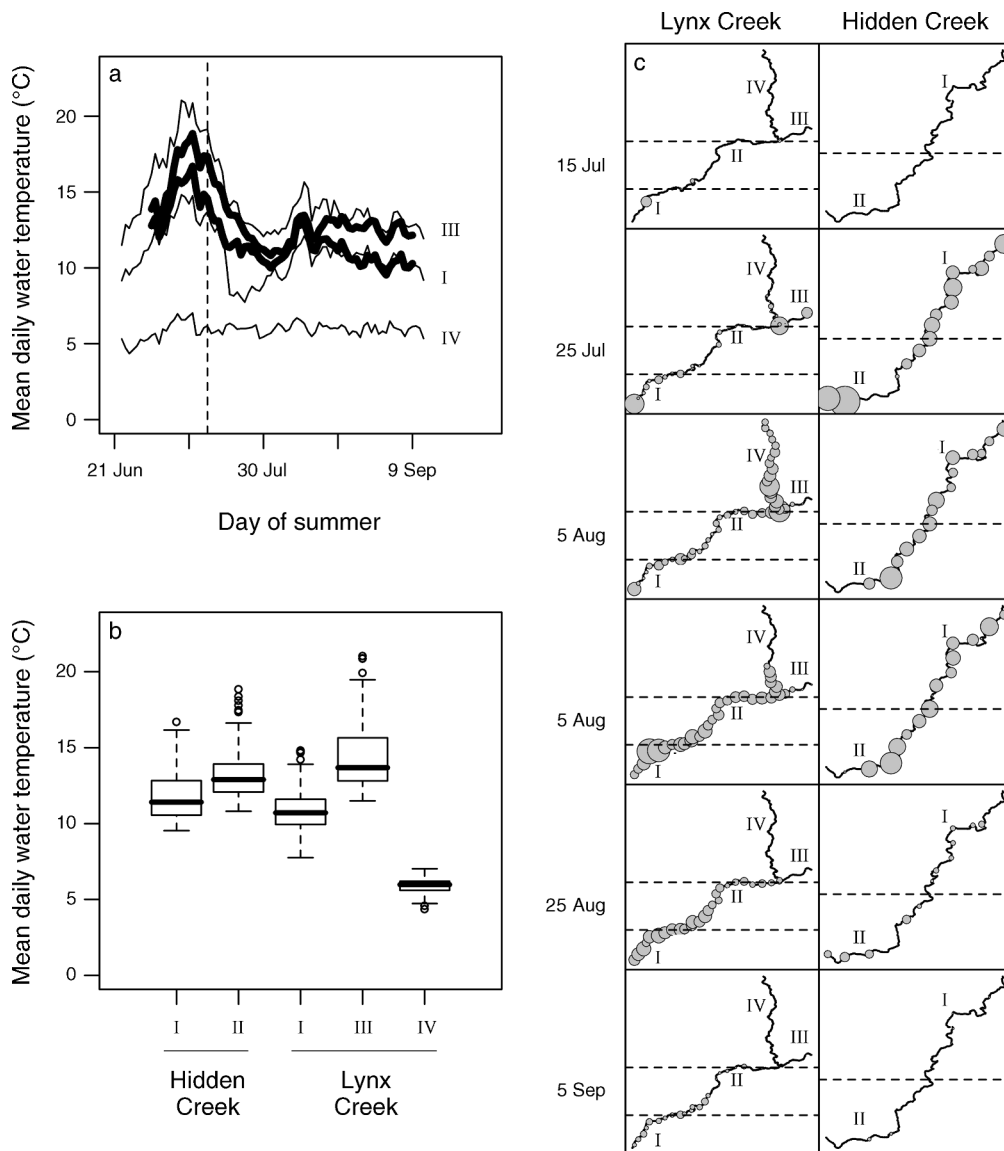


FIG. 2. (a) Summer temperature profiles in sections of Lynx Creek and Hidden Creek (bold lines) during 2009. Each line represents mean daily temperature during the summer months for a single stream section. The vertical dashed line indicates the date at which salmon spawner surveys began in each stream. (b) Boxplots of mean summer daily temperature for study sections (Roman numerals) of Hidden and Lynx Creek during 2009. Each rectangle spans the interquartile range (IQR) and shows the median as a thick line. Whiskers include data that are within $1.53 \times \text{IQR}$ of each quartile, beyond which outliers are shown as open circles. (c) Sockeye salmon distributions for Lynx Creek and Hidden Creek spanning a seven-week time period from mid-July to early September during summer 2009, quantified at 10-day intervals. Each panel represents a period of spawning since observed entry of salmon to each stream. The area of the gray circles is proportional to salmon density per 100 m of stream. Roman numerals indicate stream section and increase with distance upstream from the mouth.

bottom to top, and, unlike Lynx Creek, both sections I and II in Hidden Creek increased and decreased uniformly through time (Figs. 2c and 3a, b).

Genetic differentiation in Lynx Creek populations

We observed significant fine-scale genetic differentiation between the early- and late-spawning populations in the cold and warm reaches of Lynx Creek; this differentiation was at least as great as among spatially isolated reference populations throughout the Wood

River system (Figs. 1a, b, and 2). None of the sockeye populations in our study deviated from Hardy-Weinberg equilibrium (eight populations at 90 loci). Tests for population differentiation for all pairwise comparisons between the three Lynx Creek populations were highly significant ($P < 0.001$). Furthermore, a principal coordinates analysis of pairwise chord distances between the three Lynx Creek populations and five other populations throughout the Wood River revealed there was significant fine-scale population differentiation

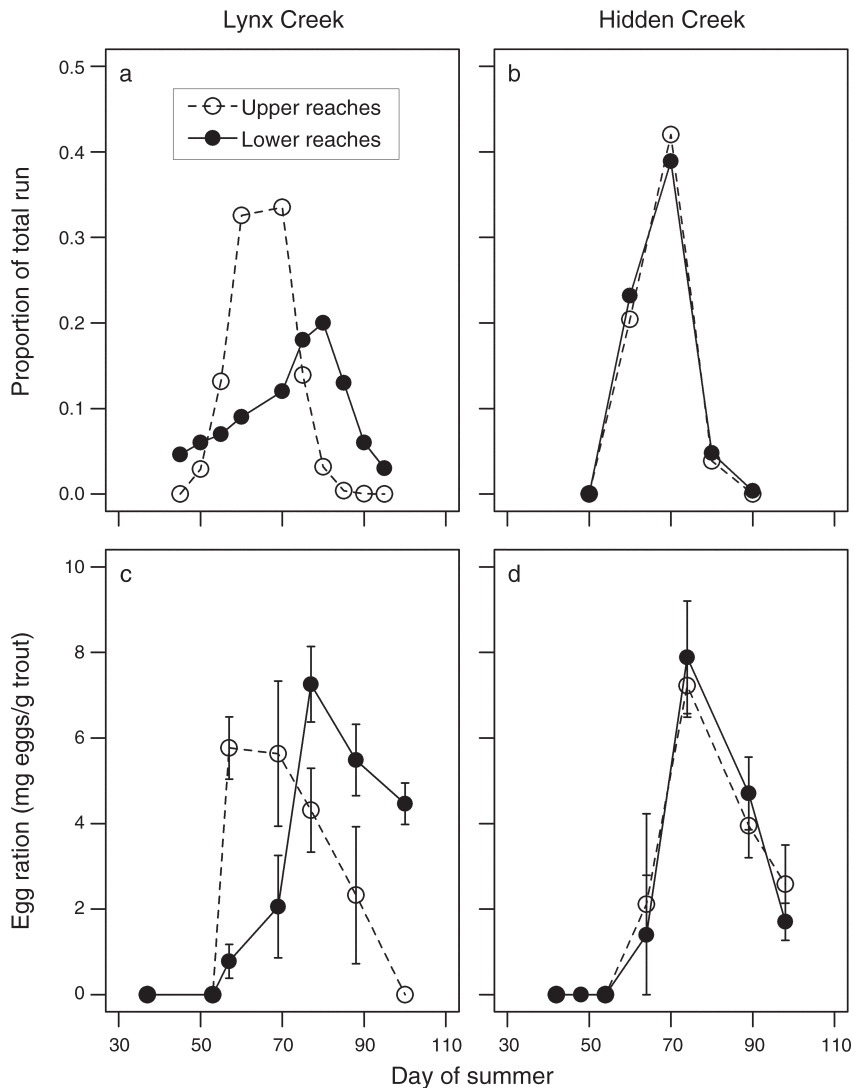


FIG. 3. (a, b) Sockeye salmon spawn timing and (c, d) mean sockeye egg ration per body mass of rainbow trout in Lynx Creek and Hidden Creek. The day of summer is equal to the number of days since 1 June; hence, the start and end dates are 1 July and 19 September, respectively. Error bars indicate \pm SE.

between the two Lynx Creek populations and the neighboring population in Lynx Lake (Fig. 1a, b). Much of this variation was due to sharp discontinuities in the frequencies of alleles at two major histocompatibility complex (MHC) class II loci, loci known to discriminate sockeye salmon populations at fine spatial scales (Gomez-Uchida et al. 2011).

Rainbow trout consumption of sockeye eggs

Variation in egg consumption by rainbow trout tracked the temporal shifts in sockeye salmon abundance observed among the segments of each stream (Fig. 3). In Lynx Creek, we observed a temporal separation of 20 d in peak egg consumption between rainbow trout sampled in the cold tributary and the main channel sections (Fig. 3c). Conversely, there was no temporal

separation in peak egg consumption by rainbow trout in Hidden Creek between each study segment. Eggs were detected in the diets of Lynx fish for \sim 43 d each season, and for 34 d each season in Hidden fish (Fig. 3d). Eggs were still found in high abundance in the diets of rainbow trout on the last sampling date of each season, so our estimate of the duration of successful predation on sockeye eggs is conservative.

Rainbow trout movement patterns in Lynx Creek

We observed strong seasonal patterns in the movements of rainbow trout in Lynx Creek coinciding with tributary-specific peak spawning period of salmon during both 2008 and 2009 (Fig. 4). In 2008, 124 out of the 191 tagged rainbow trout (64%) were detected moving across at least one antenna two or more times

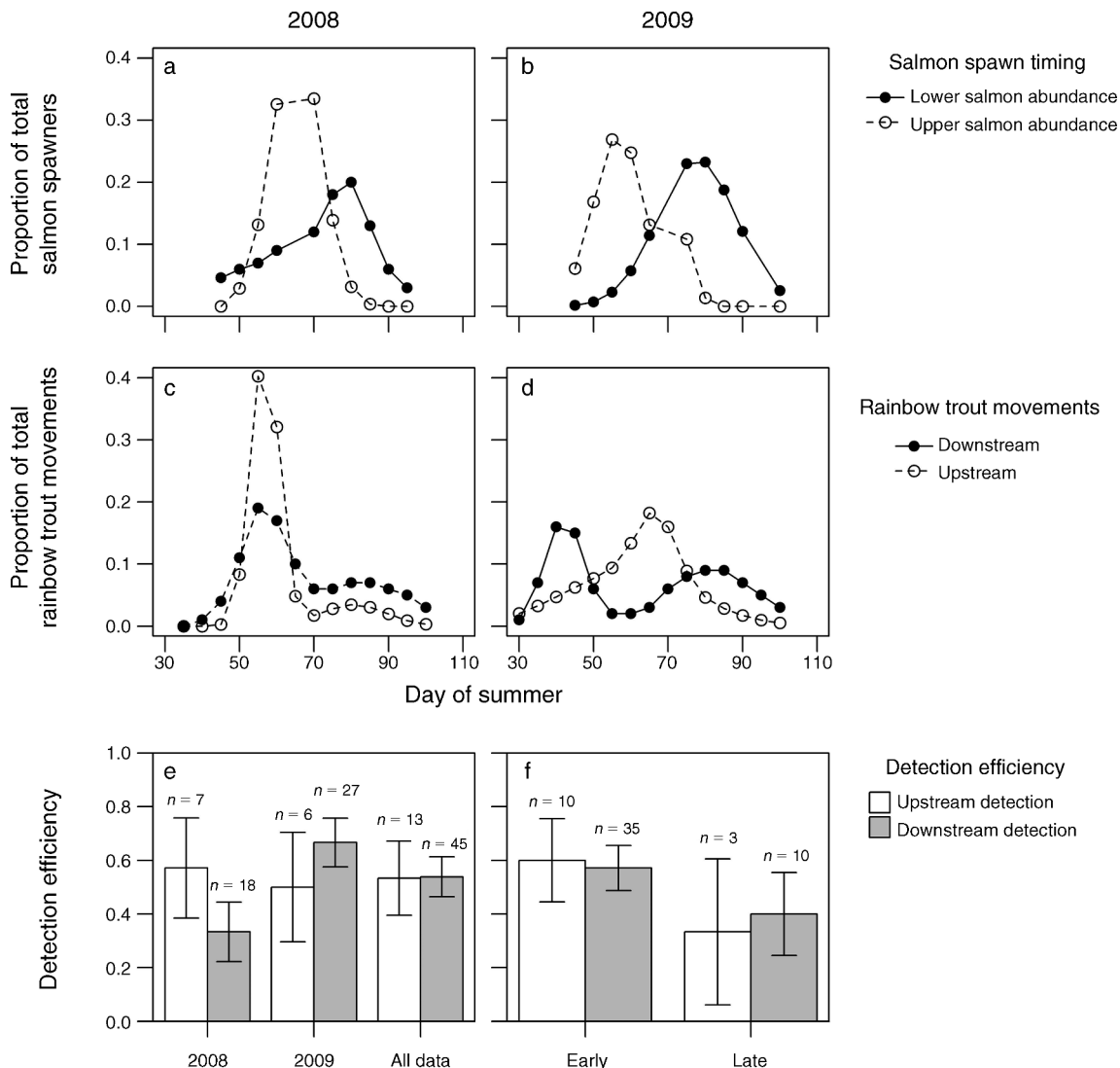


FIG. 4. Seasonal movement dynamics of rainbow trout in Lynx Creek. (a, b) Proportion of the total run of sockeye salmon in Lynx Creek stream section IV (open circles) and stream sections I and II (solid circles) in years (a) 2008 and (b) 2009. (c, d) Proportion of total number of observed upstream (open circles) and downstream movements (solid circles) by rainbow trout in Lynx Creek calculated at a five-day resolution throughout the summer in years (c) 2008 and (d) 2009. The day of summer is equal to the number of days since 1 June; hence, the start and end dates are 1 July and 19 September, respectively. (e) Calculated detection efficiencies for upstream vs. downstream movements of rainbow trout for years 2008, 2009, and combined years. (f) Calculated detection efficiencies for upstream and downstream movements of rainbow trout during early-summer (30 June–5 August) and late-summer (6 August–5 September) periods corresponding to observed peaks in upstream and downstream movements. Error bars indicate \pm SE.

throughout the summer. Of the 124 detected individuals, 45% were detected making directional upstream and downstream movements timed appropriately with the timing of peak spawning periods of sockeye salmon. In 2009, 167 out of 238 tagged rainbow trout (70%) were detected moving across two or more antennas throughout the summer, with 35% of the 167 detected individuals making directional movements timed appropriately with salmon spawning in specific stream sections.

Upstream directional movements by rainbow trout dominated during the early season (80% in 2008, and

46% in 2009), peaking in late July when sockeye spawning was focused in the cold tributary at the top of the system (Fig. 4c, d). Later in the season, downstream movements became the dominant movement pattern, coinciding with sockeye spawning in the lower reaches of the main channel. During both study years, downstream movements by rainbow trout followed a bimodal pattern having an initial early-summer peak in late July and a second peak in mid-August, coinciding with the late-summer peak of sockeye salmon in the lower main channel. For both years of the

movement study, body size did not have a significant effect on whether an individual adopted a migratory strategy (logistic regression, $P = 0.99$, $df = 259$). Finally, we detected no significant bias in detection efficiency between upstream and downstream movements of rainbow trout during both years of our study (Pearson's chi-squared, $P > 0.5$ for all pairwise comparisons; Fig. 4e, f).

Relationship between growth and movement strategy in rainbow trout

Recaptured individual rainbow trout from Hidden and Lynx Creeks (15 July through 1 September) revealed significant differences in growth between streams depending on whether rainbow trout in Lynx Creek adopted a movement or stationary strategy (ANCOVA, $F_{3,138} = 11.32$, $P < .0001$; Fig. 5). In Lynx Creek, fish that remained stationary in a single section of stream throughout the summer exhibited instantaneous growth rates similar to that of Hidden Creek fish. However, Lynx Creek fish that moved towards stream areas where salmon were actively spawning during the mid to late summer achieved significantly higher instantaneous growth rates than Hidden Creek, or stationary fish, from 1.9 times higher for 100-g fish to 2.5 times higher for a 1000-g fish (Fig. 5).

DISCUSSION

Here we show strong bottom-up benefits of landscape heterogeneity to mobile consumers. In Lynx Creek, spatial variation in water temperature (Fig. 2a, b; Appendix A: Fig. A1) is associated with population differentiation (Fig. 1b) and divergence of spawn timing (Figs. 2c and 3a) in neighboring populations of sockeye salmon. This life history diversity in sockeye salmon affected the spatial and temporal patterning of seasonal egg subsidies critical to the summer growth of rainbow trout. In Lynx Creek, the two populations of sockeye provided separate resource pulses, enabling rainbow trout to feed on eggs for at least 20 days longer than in Hidden Creek, where sockeye spawning occurred as a single pulse (Fig. 3). Finally, individual rainbow trout that moved adaptively to integrate the temporal availability of egg subsidies throughout the Lynx Creek system (Fig. 4) achieved growth rates that were roughly double those of trout that remained stationary in a single stream section throughout the summer (Fig. 5). While benefits of life history diversity in salmon to mobile consumers of salmon resources have been proposed (Schindler et al. 2010), we provide the first empirical evidence that links population diversity in salmon to benefits for mobile consumers that are able to track the spatial and temporal variation in the availability of salmon subsidies.

Population diversity in salmon is a result of local adaptation of individual populations to their natal environment (Crozier et al. 2008). It is typically assumed that population divergence occurs at larger geographic

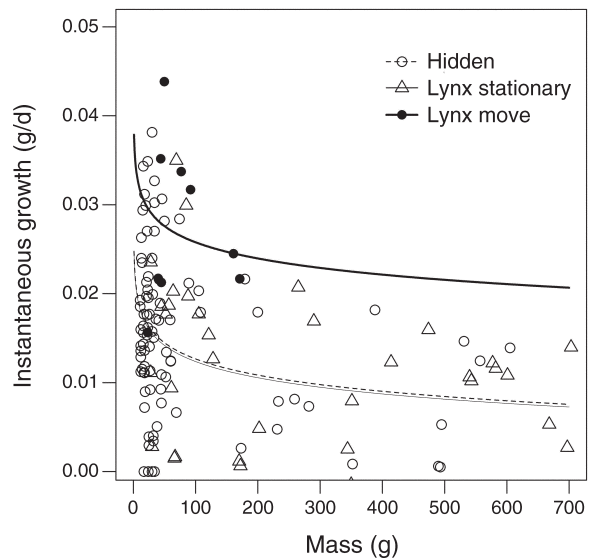


FIG. 5. Instantaneous growth as a function of body mass for rainbow trout, comparing growth rates of different categories including “Lynx move” (solid circles), “Lynx stationary” (open triangles), and “Hidden” (open circles). This figure compares instantaneous growth rates of rainbow trout from Lynx Creek that adopted “move” vs. “stationary” strategies to those captured in Hidden Creek. More specifically, “Lynx move” refers to rainbow trout from Lynx Creek that adopted movement strategies that enabled them to track the multiple pulses of sockeye eggs within Lynx Creek; “Lynx stationary” refers to those trout that did not adopt a migratory strategy and remained stationary within a single section of stream for the time they were detected within Lynx Creek; and “Hidden” refers to rainbow trout captured in Hidden Creek that are comparable to “Lynx stationary” trout because there is only a single run of sockeye to Hidden Creek. Curves were generated using estimated intercepts for each category using ANCOVA ($F_{3,138} = 11.32$, $P < 0.0001$).

scales. Consistent with the findings of previous studies on thermally mediated phenotypic and genotypic divergence in salmon (Tallman 1986), we show that ecologically important divergence in salmon occurs at the within-stream scale associated with spatial variation in water temperature (Figs. 1 and 2). Other examples exist in nature where organisms such as parasites (Criscione and Blouin 2007), zooplankton (Geedey et al. 1996), and other fishes (Warnock et al. 2010) exhibit genetic differentiation through local adaptation at equally fine or finer spatial scales than we have observed with salmon. Because of the fine-scale genetic diversity observed in salmon populations, landscape heterogeneity at fine spatial scales (<2 km) is likely important in producing population divergence in salmon. In the Wood River, population differentiation is associated with variation in the spawn timing of sockeye salmon populations among the many streams, rivers, and lakes of the system (Marriott 1964). This variation extends the potential time in which salmon resources are available to mobile consumers, from ~3 weeks to >2.5 months (Schindler et al. 2010). Population differentiation of

salmon is associated with strong thermal gradients within Lynx Creek, and mobile consumers (rainbow trout) have adopted movement strategies that enable them to track and extend the availability of high-quality food resources to increase their seasonal growth rates. We suspect that other predators and scavengers such as bears, gulls, and eagles are also tracking changes in the availability of sockeye resources throughout the Wood River system, much like the rainbow trout in Lynx Creek.

There are other examples of mobile consumers benefiting from behavioral adaptation to spatial and temporal heterogeneity in resources (Vanschaik et al. 1993, Klaassen et al. 2006, Oliver et al. 2010). Resource tracking across heterogeneous landscapes by mobile consumers has been previously documented in terrestrial systems. For example, ungulates have been shown to track hotspots of high resource quality by following gradients in plant phenology over large distances (Fryxell and Sinclair 1988, Boone et al. 2006, Wang et al. 2006). However, there are few studies providing actual empirical evidence that consumers benefit from heterogeneity in their prey. Wang et al. (2006) showed that density dependence in herbivores was weaker in years when the spatial heterogeneity in vegetation was higher. Searle et al. (2010) showed through experiments that migratory grasshoppers had increased growth when vegetation availability was heterogeneous in space and time. Here we provide the first empirical evidence of this phenomenon in an aquatic ecosystem, showing that population diversity in sockeye salmon extends foraging opportunities for rainbow trout due to spatiotemporal heterogeneity in resource availability. While there is strong evidence that the phenotypic diversity among sockeye salmon populations in our study is genetically based, similar benefits to predators may arise from variation in prey populations produced by phenotypic plasticity.

Spatial variation in both stream temperature and the availability of salmon subsidies may reduce density-dependent effects of resource availability on rainbow trout compared to conditions where both water temperature and the availability of egg subsidies are spatially homogenous through time. Wang et al. (2006) showed that increasing spatial variation in the availability of vegetation reduced the strength of density dependence on mobile ungulate consumers in terrestrial ecosystems by increasing the temporal availability of quality food resources. Partial migration within a population may increase the overall carrying capacity of available habitat by allowing consumers to exploit resources over a larger spatial extent compared to situations where all organisms moved adaptively to exploit spatial and temporal variation in high-quality resources. During both years of our Lynx Creek movement study, we observed between 35% and 45% of tagged and detected rainbow trout making directed movements towards sockeye spawning areas. While it is plausible that

moving vs. stationary rainbow trout represent distinct populations, this possibility is discounted by the lack of genetic divergence observed between sympatric populations of anadromous and resident rainbow trout within a single drainage due to hybridization (Narum et al. 2004). The fish that adopted a movement strategy also had significantly higher growth rates, indicating net energetic benefits to this strategy. The fact that only a subset of individuals adopted this directed movement strategy suggests there are fitness trade-offs associated with moving to capitalize on salmon subsidies such as territory defense, vulnerability to predators, or energetic costs. Our findings are supported by previous work on juvenile coho salmon that showed only a fraction of the tagged population moved at least one stream habitat unit (28–60%), even though there were clear growth benefits associated with movement (Kahler et al. 2001). Additionally, our findings that body size did not influence the probability of movement by rainbow trout further suggests that there are substantial costs associated with moving across large areas of stream. Nonetheless, partial migration by rainbow trout in our study appears to have allowed individuals that moved to track sockeye salmon resources to increase their growth rates.

The link between biodiversity and ecosystem functioning has been studied extensively (MacArthur 1955, Hooper et al. 2005). However, fewer studies have assessed the effects of intraspecific diversity on ecosystem processes and services (Luck et al. 2003). Local adaptations of sockeye salmon to natal watersheds has ultimately reduced the variation in total annual returns of this commercially important species across Bristol Bay (Hilborn et al. 2003). At the watershed scale, long-term variation of sockeye salmon returns to the aggregation of all streams of the Wood River system combined has been significantly less variable than that of individual stream populations (Schindler et al. 2010). For mobile consumers of salmon resources including bears, birds, and rainbow trout, the stabilizing effect of population diversity on the annual return of salmon to the Wood River system ensures consistency of this key food resource from year to year. Exploitation of salmon resources by trout also provides economic services to humans, as rainbow trout are the target of a rapidly growing recreational fishery in Bristol Bay watersheds worth up to U.S.\$152 million, roughly half the value of the commercial salmon fishery (Duffield et al. 2006). Therefore, management of diversity in salmon affects the services they provide to both the recreational fishery for rainbow trout and the commercial salmon fishery; culturally, economically, and socially important industries in the Bristol Bay region of Alaska.

In summary, we demonstrate the importance of landscape heterogeneity in mediating important ecological processes in aquatic systems and how subtle habitat diversity generates important intraspecific life history variation that mediates interactions between resource

suppliers and consumers. Population diversity in sockeye salmon has undoubtedly provided important benefits to rainbow trout and other consumers of salmon resources, and ultimately the biological integrity of ecosystems upon which much of the local human economy is based. Management goals for imperiled species are increasingly focused on conserving critical ecological processes within an ecosystem context (Levin and Lubchenco 2008). Our results highlight the need for more appropriately scaled research to understand how ecological processes are controlled by landscape heterogeneity, and how overall ecosystem functioning is dependent on this complexity (e.g., Fryxell et al. 2005).

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APPENDIX A

Thermal characteristics of Lynx Creek and Hidden Creek for study years 2008 and 2009 (*Ecological Archives* E092-181-A1).

APPENDIX B

Comparison of temporal changes in sockeye salmon spawner distributions across years (*Ecological Archives* E092-181-A2).

APPENDIX C

Description of molecular genetics methodology using SNPs (*Ecological Archives* E092-181-A3).

APPENDIX D

Description of methodology used in quantitative assessment of rainbow trout diets (*Ecological Archives* E092-181-A4).

APPENDIX E

Analysis of antenna detection efficiency of directional rainbow trout movements (*Ecological Archives* E092-181-A5).